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Distribution, Reproduction, and Shell Growth of Limpets in Port Valdez, Alaska

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Abstract. This study documents the distribution of six limpet species occurring in Port Valdez, Alaska, and the reproductive cycle and shell growth patterns for one of those species, *Tectura persona* (Rathke, 1833). The distribution of the limpets observed in Port Valdez shows similarities to that described for the same species elsewhere. The abundance of *Tectura fenestrata* (Reeve, 1855) was associated with changes in environmental variables suggesting downward migration or increased cryptic behavior in winter. Reproductive activity (including developmental stages) was present in *T. persona* throughout the year. Shell growth of *T. persona* appears to be relatively slow and the longevity of limpets moderate. During this study, no effects of oil contamination on limpet abundance were apparent for limpets near an oil terminal.

INTRODUCTION

Limpets are a common component of the intertidal fauna along the north Pacific coast but little is known about the life history of these limpets in Alaskan waters. The oil spill following the grounding of the *Exxon Valdez* in March 1989 within Prince William Sound, Alaska, highlighted the importance and lack of biological information for the intertidal fauna throughout the sound. Six intertidal limpet species occur in Port Valdez, a fjordic embayment in Prince William Sound, as well as on rocky shores throughout the rest of the sound. These species are of two families (Lindberg, 1986): family Acmaeidae with the single species *Acmea mitra* (Rathke, 1833) and family Lottiidae including the five species *Lottia borealis* (Lindberg, 1982), *L. pelta* (Rathke, 1833), *Tectura fenestrata* (Reeve, 1855), *T. persona* (Rathke, 1833), and *T. scutum* (Rathke, 1833) (D. Lindberg, personal communication).

Investigations of lottiid and acmaeid limpets in other regions of the north Pacific have considered the same species as those occurring in Port Valdez. The tidal ranges occupied by these six species elsewhere along the Pacific Coast are well described: *A. mitra* is a low intertidal species, *L. borealis* and *L. pelta* both occur in the low to high intertidal, *T. persona* occurs in the mid to high intertidal, and *T. fenestrata* and *T. scutum* are found in the low to mid intertidal zone (Fritchman, 1961a, b, c, 1962; Lindberg, 1981, 1982, 1986). Reproductive studies demonstrate that *T. fenestrata* and *T. persona* in central California are reproductively active in fall and winter, whereas *L. pelta* and *T. scutum* are reproductively active year-round (Fritchman, 1961b, c, 1962). Fritchman (1961b, 1962) suggested that higher summer temperatures limit reproductive activity in *T. fenestrata* and *T. persona* in California. Shell growth of these six limpets is not well described. Frank (1965a, b) found that size alone cannot be used to estimate age or longevity in limpets due to the wide size range found in any particular age class. Kenny (1968) came to the same conclusion for *T. persona* from Oregon. Branch (1981) highlighted the inverse relationship between growth rate and longevity and indicated that slower growing limpets tend to live longer.

Port Valdez is the terminus of the pipeline transporting crude oil from the North Slope region of Alaska. Concern for the health of the intertidal community in the vicinity of the terminal prompted investigations of the life history of dominant intertidal organisms (Rucker, 1983; Feder & Keiser, 1980; Feder & Bryson-Schwafel, 1988; Blanchard & Feder, 1997, 2000). Because it is known that patellid limpets are highly susceptible to oil contamination (e.g., Smith, 1968; Thompson, 1980), the importance of understanding the biology of limpets in Port Valdez was recognized. Additionally, studies emerging after the *Exxon Valdez* oil spill demonstrated that *T. persona* was the species most affected by petroleum contamination (Highsmith et al., 1996; Hooten & Highsmith, 1996). However, the life history of this limpet in Alaskan waters was not readily available to these investigations. This study documents the distribution of the dominant intertidal limpets and focuses on the reproductive biology and shell growth of *T. persona* in Port Valdez, Prince William Sound, Alaska, an area not affected by the *Exxon Valdez* oil spill.

METHODS

Study Site

Port Valdez is a subarctic glacial fjord located in the northeastern corner of Prince William Sound, Alaska

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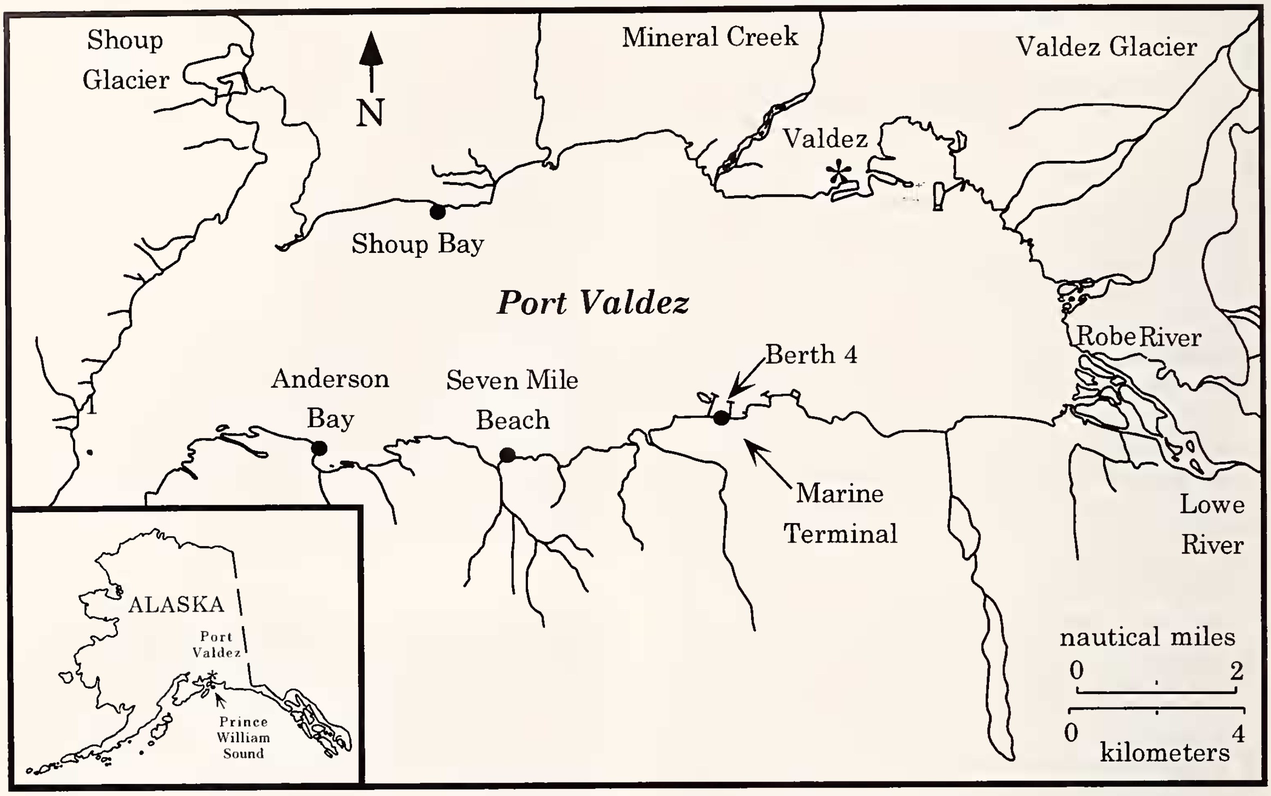


Figure 1

Map of sampling locations in Port Valdez, Alaska. Sampling locations are indicated with a large dot.

(Figure 1). It is approximately 22 km long by 5 km wide and is surrounded by the mountains of the Chugach range. The intertidal region is composed of rocky shores in the west, grading to extensive mudflats in the eastern end of the fjord (Blanchard & Feder, 1997). The mean air temperature ranges from 13°C in summer to −10°C in winter (Hood et al., 1973). Surface-water temperatures range from 16°C in summer to −2°C in winter (Jewett & Feder, 1977). Mean annual precipitation is 158 cm. During summer, positive estuarine flow results in increased sediment loads and decreased salinity (approaching 0‰ at some locations). During winter, estuarine circulation ceases as freshwater inputs decrease and salinity rises. Most of the annual primary productivity (150–200 g C m^{-2} y^{-1}) occurs in April and May (Goering et al., 1973). The fjord receives greatly decreased amounts of light in winter (less than 7 hours from mid November through February) and the angle of incidence for sunlight is very low. Additionally, Port Valdez is oriented in an east-west direction and the surrounding mountains shade much of the fjord. Thus, in winter, water-column and benthic primary productivity is very limited. Port Valdez is a relatively sheltered environment, and winds and storms inside the fjord are the primary sources of wave action. Average monthly wind speeds usually range from 3 to 16 km h^{-1}. However, peak winds up to 64 km h^{-1} are commonly observed in winter, and peak winds up to 145 km h^{-1} are occasionally observed (NOAA Weather Service, Valdez, Alaska).

Table 1

Spearman rank correlations between measured environmental variables. The critical level for significance testing is the Bonferroni corrected $\alpha^* = 0.0083$.

	Air temperature	Water temperature	Salinity
Water Temperature	0.84**	—	—
Salinity	− 0.83**	− 0.77**	—
Suspended Sediment	− 0.61**	ns	0.43*

* $0.0001 \leq P \leq 0.0083$, ** $P < 0.0001$.

Four intertidal sites were sampled monthly for limpets from September 1988 to September 1990 (Figure 1). Sampling was not performed in some months due to inclement weather. These sites, 7 Mile Beach—7M, Anderson Bay—AB, Berth 4—B4 (within the confines of the marine terminal), and Shoup Bay—SB, composed

Table 2

Limpet abundance (mean ind. m^{-2}) and standard errors (SE) for selected tidal heights (Stakes 4–11) for four stations from Port Valdez. *T. persona* = *Tectura persona* and *T. fenestrata* = *Tectura fenestrata.*

			T. persona		*T. fenestrata*		*Lottia* species		Juveniles	
Site	Year	Month	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7M	1988	October	79	15.3	70	10.1	47	7.7	67	12.7
	1989	February	11	3.9	39	9.0	49	9.7	35	7.8
		April	34	12.6	59	13.9	53	13.4	22	8.2
		July	64	12.9	139	22.8	83	15.7	17	7.1
		October	28	10.8	102	25.8	34	11.7	16	5.7
	1990	April	31	6.4	87	21.6	23	7.4	19	5.4
		July	66	15.2	193	36.1	27	7.5	93	39.8
		September	70	15.1	164	25.9	33	16.5	133	38.6
AB	1988	October	109	16.4	82	12.1	66	10.8	27	7.0
	1989	February	47	10.0	22	6.4	43	8.0	4	1.3
		April	76	15.5	21	6.9	44	7.4	10	4.2
		July	39	10.8	80	22.7	68	15.6	29	16.3
		October	91	29.7	92	18.9	34	8.8	8	7.8
	1990	April	93	12.6	73	15.9	36	8.5	17	5.6
		July	91	14.9	130	17.9	40	9.7	149	55.2
		September	74	16.5	169	22.1	38	5.8	176	97.1
B4	1988	October	20	5.8	49	7.7	14	4.7	41	7.1
	1989	February	9	4.1	59	10.1	23	4.6	30	7.3
		April	20	9.3	77	21.6	23	7.6	16	4.0
		July	14	4.5	56	10.0	44	10.1	20	7.9
		October	31	13.8	76	18.3	33	9.8	11	4.2
	1990	April	24	5.1	34	8.0	4	1.7	5	1.8
		July	25	6.8	78	9.7	11	3.3	1	0.6
		September	43	8.1	79	13.0	21	6.0	6	2.1
SB	1988	October	95	14.5	94	15.9	42	7.8	34	6.7
	1989	February	8	2.9	69	13.6	46	8.3	43	8.2
		April	14	8.4	44	12.3	55	19.3	2	1.7
		July	45	11.7	113	27.1	144	30.0	116	44.3
		October	13	5.5	106	37.8	11	5.0	30	11.6
	1990	April	66	12.3	106	22.0	24	8.2	17	4.8
		July	24	7.0	163	33.9	19	5.5	6	3.4
		September	22	6.4	199	39.7	17	4.7	12	4.8

part of a concurrent environmental study of the intertidal region in Port Valdez (Jewett et al., 1993). Sampling areas within the four sites were selected based on high abundance values of limpets. The selection bias toward high abundance of limpets was necessary to ensure adequate numbers of limpets for all components of the study. Limpets are present in all rocky intertidal areas of Port Valdez but often occur in low densities. The intertidal regions were roughly classified as high intertidal if the vertical distance from mean lower low water was 2 m or greater, mid intertidal if the distance was between 1 to 2 m, and low intertidal if the distance was less than 1 m. The 7M site was a gently graded cobble beach with a small rock face in the high intertidal. The AB site was primarily a rock face and small ridge with boulders and small rocks in the mid intertidal and gravel in the low intertidal. SB was a moderately graded beach composed of smaller rocks at lower elevations grading to large rocks in the high intertidal. The B4 site was composed of a short, moderately graded rocky beach in the low to mid-intertidal grading up to boulders and loose gravel in the high intertidal. Other than the six limpet species, *Acmea mitra, Lottia borealis, L. pelta, Tectura fenestrata, T. persona,* and *T. scutum,* no other species were identified from Port Valdez. *Lottia digitalis* (Rathke, 1833) is described for western Prince William Sound (Highsmith et al., 1996) but was not found during this study in Port Valdez.

Sampling and Analytical Procedures

Surface-water temperature, salinity, suspended sediment, and air temperature were measured during sam-

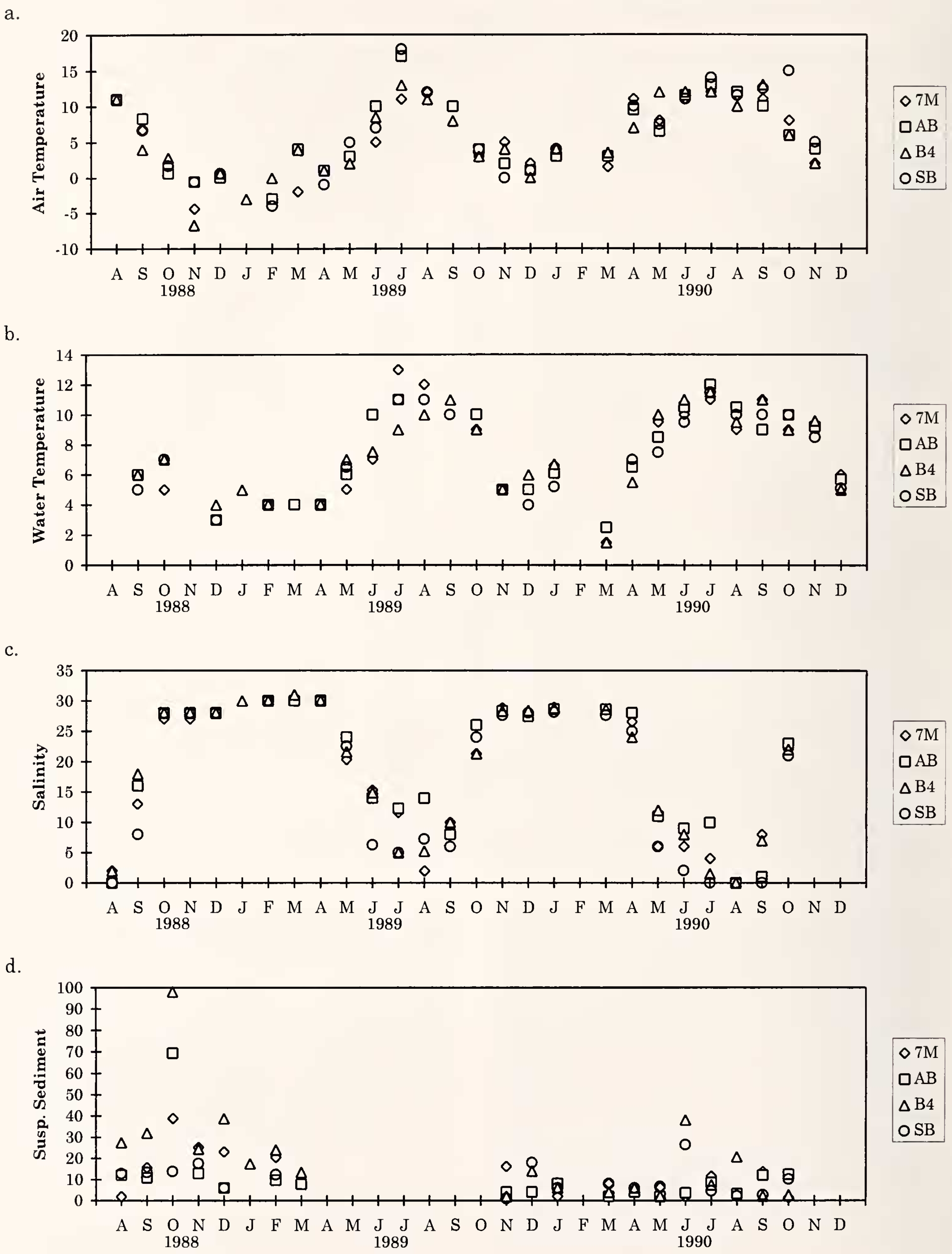

a.
Air Temperature
20
15
10
5
0
-5
-10
b.
Water Temperature
14
12
10
8
6
4
2
0
c.
Salinity
35
30
25
20
15
10
5
0
d.
Susp. Sediment
100
90
80
70
60
50
40
30
20
10
0
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1988
1989
1990
◇ 7M
□ AB
△ B4
○ SB

Table 3

Spearman rank correlations between monthly average counts of limpets at each tidal height sampled. The critical level for significance testing is the Bonferroni corrected $\alpha^* = 0.0056$.

	Tectura persona	*Tectura fenestrata*	*Lottia* species
Tectura fenestrata	− 0.11*	—	—
Lottia species	ns	0.59**	—
Juveniles	− 0.30**	0.59**	0.53**

* $0.0001 \leq P < 0.0083$, ** $P < 0.0001$.

Table 4

Spearman rank correlations between monthly average counts of limpets by species and measured environmental variables. The critical level for significance testing is the Bonferroni corrected $\alpha^* = 0.0031$.

	Tectura persona	*Tectura fenestrata*	*Lottia* species	Juveniles
Air Temperature	ns	0.50**	ns	ns
Water Temperature	ns	0.68**	ns	ns
Salinity	ns	− 0.64**	ns	ns
Suspended Sediment	ns	ns	ns	ns

* $0.0001 \leq P < 0.0083$, ** $P < 0.0001$.

pling at each site. Water samples for suspended sediment and salinity were collected at low tide from the shoreline. Salinity measurements were determined using a portable American Optical compensated salinity refractometer. In the laboratory, the water samples were filtered on pre-weighed 0.45 mm Millipore filters. The filters were dried to a constant weight at 60°C and suspended sediments calculated (mg l^{-1}).

Transects were established at each site and sampled at permanently marked points separated by a 40 cm vertical distance. Intervals along the transect were marked starting from the upper edge of the lichen (*Verrucaria* species) zone in the high intertidal down to the lowest tidal height available in May 1988. The tidal heights (m) of each sampling location were calculated from predicted tide heights (NOAA tide tables). Four to eight 0.04 m^2 quadrants were sampled at each marked interval by a random toss of a 20 × 20 cm sampling frame onto the substrate. The number of limpets of each species observed in the frame was recorded. Within Port Valdez, some of the dominant limpets are cryptic so sampling included searching underneath rocks and crevices observed within the sampling frame. For abundance estimates, densities of *Lottia pelta* and *L. borealis* were recorded as *Lottia* species due to difficulties in separating the two species in the field. Additionally, no attempt was made to identify juvenile limpets (< 5 mm) to species. Since the abundance data were too numerous to present, plots of limpet abundance were made for two selected tidal height ranges—0.35 to − 0.15 m CD and 2.05 to 2.25 m CD, representing the abundance of limpets at a high and low tidal range. However, the full data set was utilized for other analyses.

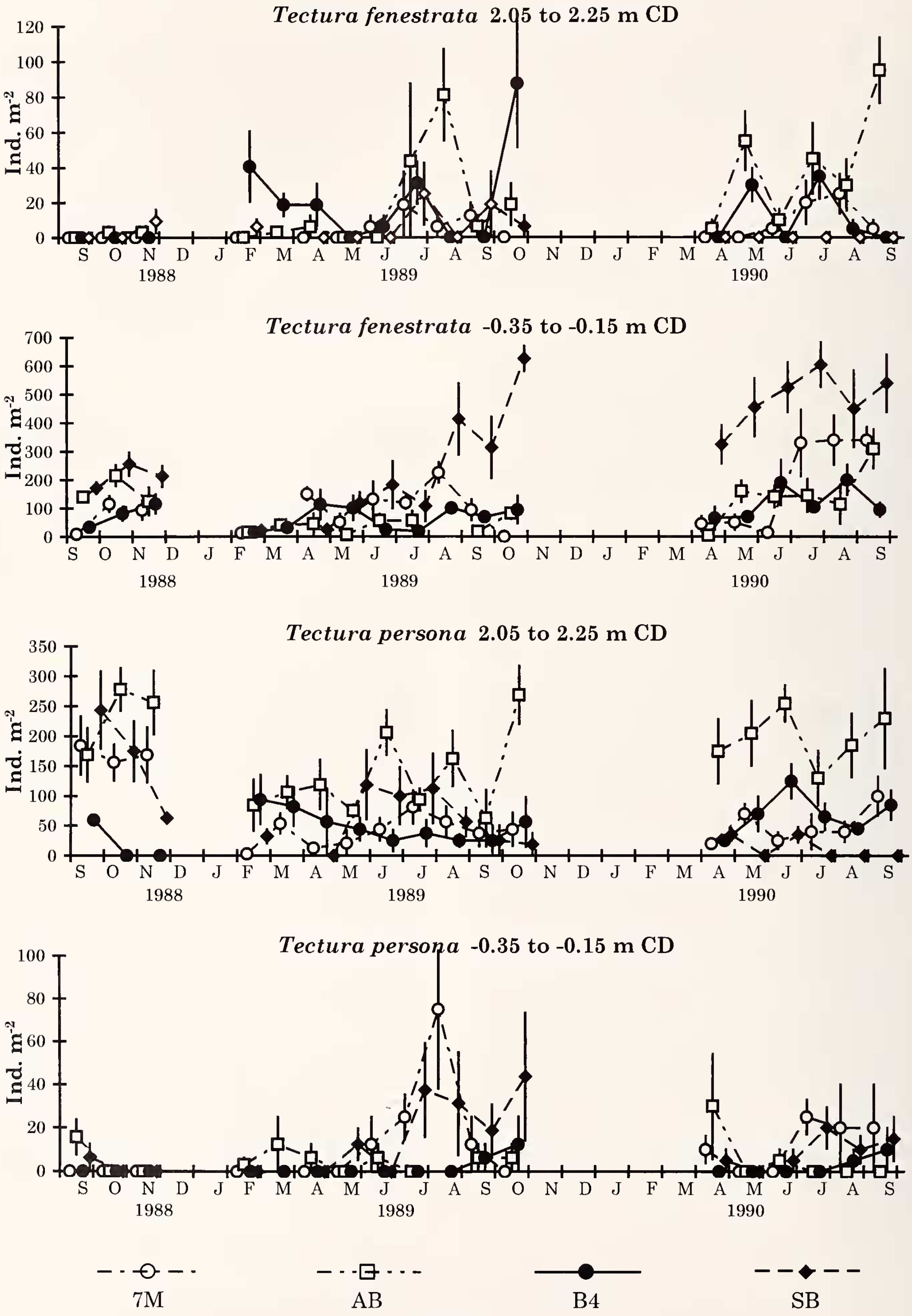
Stereological methods were applied to assess the reproductive cycle of *T. persona.* Up to 12 limpets were processed for each site from every sampling period although numbers varied due to sampling difficulties. Limpets were preserved in Baker's Formal-Calcium in the field and stored in 70% ethyl alcohol in the laboratory. Histological preparation of reproductive tissues followed procedures outlined by Lowe et al. (1982). Up to 20 follicles from a limpet were classified by stereological observation, and the reproductive stage of an individual was assigned as the category containing the greatest count of follicles. The tissues were placed within the following categories adapted from Orton et al. (1956): Neuter (no identifiable reproductive tissues); Developing (small developing reproductive tissues in which developing orange-colored eggs or cream-colored sperm were observable); Ripe (the gonad is thick and swollen; orange eggs are compressed and polygonal in shape and sperm fills the male follicles); Spawning (eggs round due to release of some gametes and male follicles show space in the center where sperm has been released); and Spent (only residual eggs or sperm are present).

Limpets were sampled for growth and age measurements at every tidal height at the study sites in March and June 1990 using the quadrant-sampling method described above. Total length of limpets was measured (± 0.01 mm) using a video image analysis unit (consisting of a video camera attached to a dissecting scope and to a digitizer pad for measurements). Limpets were aged by counting the major growth disruption rings on shells. The age of a limpet was taken to be the sum of the observed growth rings. Since movement of a limpet to the next age class would occur with the onset of new growth, an age-0 limpet (limpets settling in winter/early spring) would have a shell composed of up to one season's worth of

←

Figure 2

Plots of environmental variables from the four sites in Port Valdez, Alaska. The plot labeled a is air temperature (C°), b is surface-water temperature (C°), c is salinity (‰), and d is suspended sediment (mg L^{-1}).



Tectura fenestrata 2.05 to 2.25 m CD

Tectura fenestrata -0.35 to -0.15 m CD

Tectura persona 2.05 to 2.25 m CD

Tectura persona -0.35 to -0.15 m CD

Figure 3

Abundance (ind. m^{-2}) of *Lottia* spp., juveniles, *Tectura fenestrata,* and *T. persona* at four sites from Port Valdez, Alaska. Error bars are ± 2 standard errors.

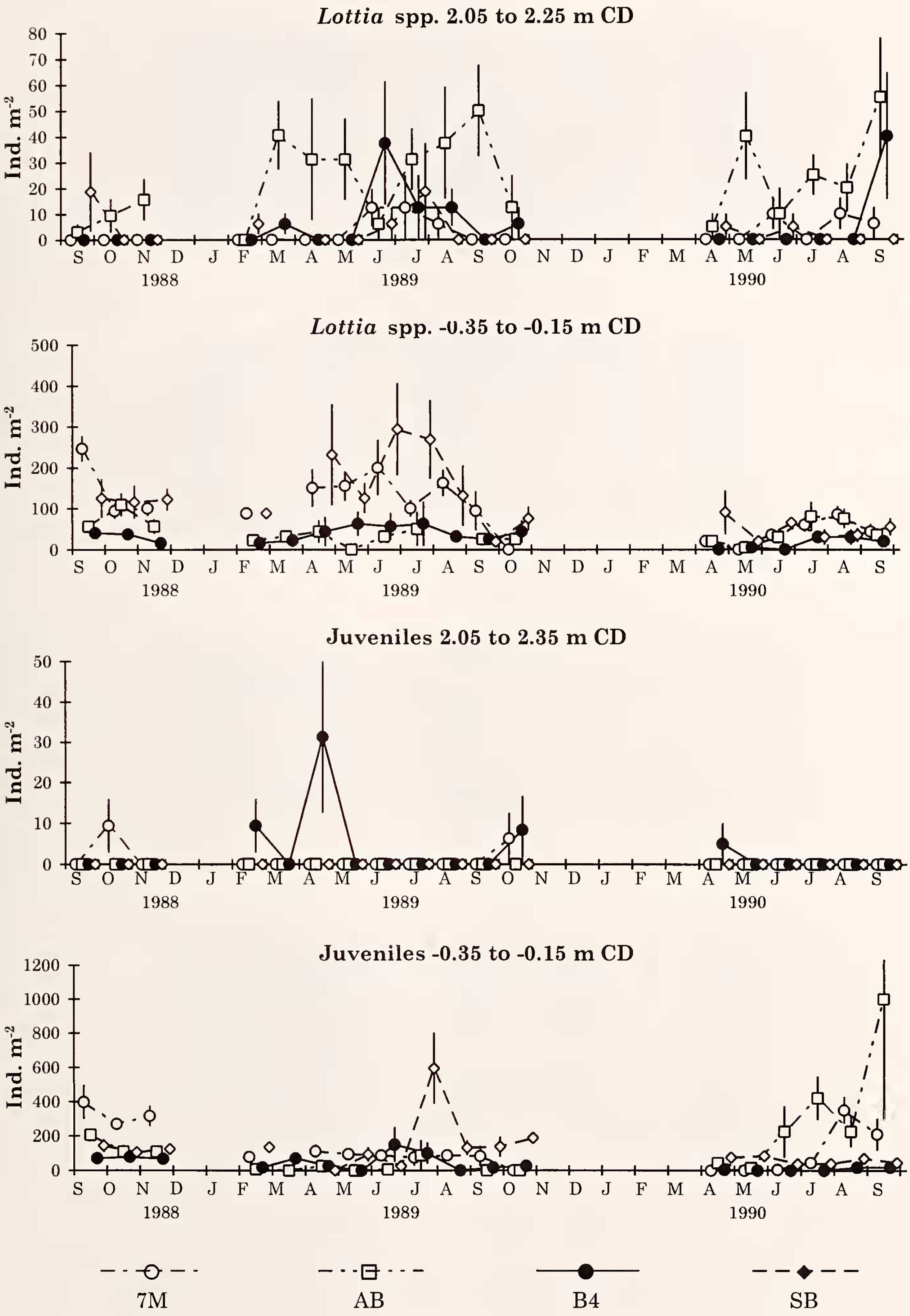


Figure 3

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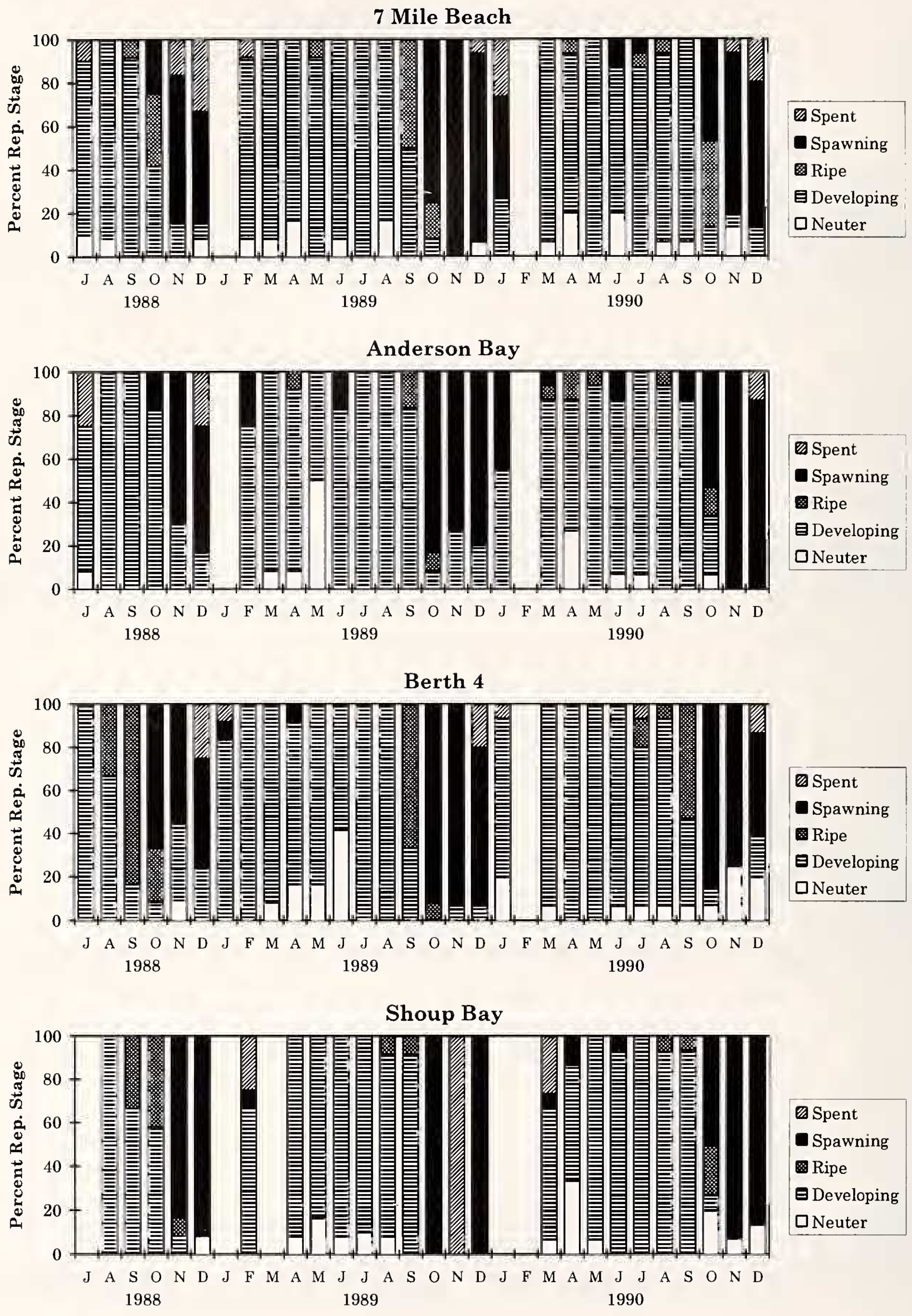

Figure 4

Bar charts of percent reproductive stage of *Tectura persona* by month for the four sites in Port Valdez, Alaska.

Table 5

Summary of regression analysis of estimated age and growth of *Tectura persona* from sites in Port Valdez. n = 812.

	Coefficient	SE	t-statistic	*P*-value
Intercept 7M, SB	2.49	0.207	12.07	< 0.0001
Slope 7M, B4, SB	1.63	0.038	42.34	< 0.0001
Intercept AB	1.71	0.410	4.17	< 0.0001
Intercept B4	0.36	0.154	2.31	0.0211
Slope AB	− 0.31	0.073	− 4.22	< 0.0001

growth with no obvious growth ring. Movement to subsequent age classes occurs with the onset of new growth. Although preliminary marking studies (Feder et al., 1992) were not entirely conclusive in determining whether rings on limpet shells represented annual growth, these rings were the best available estimate of limpet age. Regression analysis includes regression of limpet length against tidal height and estimated age for each site.

Data Analyses

The analyses of the abundance and reproductive data are primarily descriptive. The cryptic behavior of some species made accurate abundance estimates impossible, and abundance data are presented as means and standard errors. Nonparametric correlation analyses were performed to assess associations between environmental variables and limpet abundance with data from all sites combined. The significance level of the correlation analyses were corrected for the number of comparisons by the Bonferroni correction of $\alpha^* = \alpha/n$ where $n = \#$ comparisons made.

Growth data were analyzed using linear regression procedures. Preliminary analysis of the growth to age relationship for *T. persona* indicated an extremely shallow concave growth curve, and nonlinear regression estimation procedures could not adequately fit the von Bertalanffy model, a normal model for limpet shell growth (Branch, 1981), to the data. Initial linear regression analyses indicated only slight deviations from the linear model at the extremes of the growth measurements. Thus, growth is modeled using linear regression (Neter et al., 1990) as an approximation to the very shallow, concave growth curve of limpets in Port Valdez. The potential for bias in the regression coefficients due to errors in the estimation of age of limpets was recognized. Nevertheless, the regression analyses are presented to provide a descriptive framework useful for future investigations.

Data files pertaining to this study may be accessed on the World Wide Web at www.veliger.org.

RESULTS

Seasonal trends in environmental conditions exhibited marked extremes (Figure 2). Air temperatures measured at the time of sampling ranged from − 6.7°C to 18°C and surface-water temperatures from 1.5°C to 13.0°C. Salinity ranged from 0% to 31‰ and turbidity from 1 mg L^{-1} to 98 mg L^{-1}. ANOVA comparisons of the environmental variables indicated no significant differences ($p < 0.05$) in mean values between sites over the course of the study. Correlation analysis of environmental variables indicated significant positive correlations ($p < 0.0083$) between air and water temperatures, negative correlations for both air and water temperatures to salinity, a low positive correlation of suspended sediment with salinity, and a negative correlation of suspended sediment with air temperature (Table 1).

Field observations indicate distinct behavioral patterns for some of the limpets in Port Valdez. *Tectura persona* exhibits negative phototactic and strongly reclusive behavior and feeds primarily after sunset and before sunrise. During low tides in daylight hours, *T. persona* typically aggregates under rocks or in crevices near boulder bases. *Tectura fenestrata* becomes abundant at tidal heights where *T. persona* abundance decreases, and inhabits areas such as small crevices, the undersides of rocks in cobble beaches, and spaces within mussel clumps which afford it additional protection against thermal stress and desiccation. Unlike *T. persona,* other limpet species (*Lottia* species and *T. fenestrata*) did not exhibit negative phototactic behavior nor were they as strongly reclusive, but all limpets appeared to avoid extreme weather conditions by moving into crevices or under rocks.

Limpet abundance data revealed only broad trends in abundance related to tidal height. *Lottia* species and *T. fenestrata* were observed from the lower to high tidal heights with greatest abundance in the lower and mid-intertidal regions, whereas *T. persona* was more common in the high intertidal zone (Figure 3). The abundance data show that juveniles generally appeared in early to mid summer predominantly at lower tidal heights (Figure 3). *Acmea mitra* and *T. scutum* were observed during the study in extremely low abundance at the lower tidal heights. Seasonal abundance trends were only marginally apparent as there appeared to be an increase in abundance through the summer to late fall with lower abundance of all limpets in the winter; however, the trends are not consistent (Table 2 and Figure 3). Means and 95% confidence intervals for abundance data did not reveal patterns reflective of site-to-site differences. Correlation analyses of mean monthly limpet abundance (ind. m^{-2} per tidal height) revealed a significant ($p < 0.0083$) positive correlation between *Lottia* species and juveniles, positive correlations of *T. fenestrata* abundance to *Lottia* species and to juveniles, and low negative correlations of *T. persona* to *T. fenestrata* and to juveniles (Table 3). Corre-

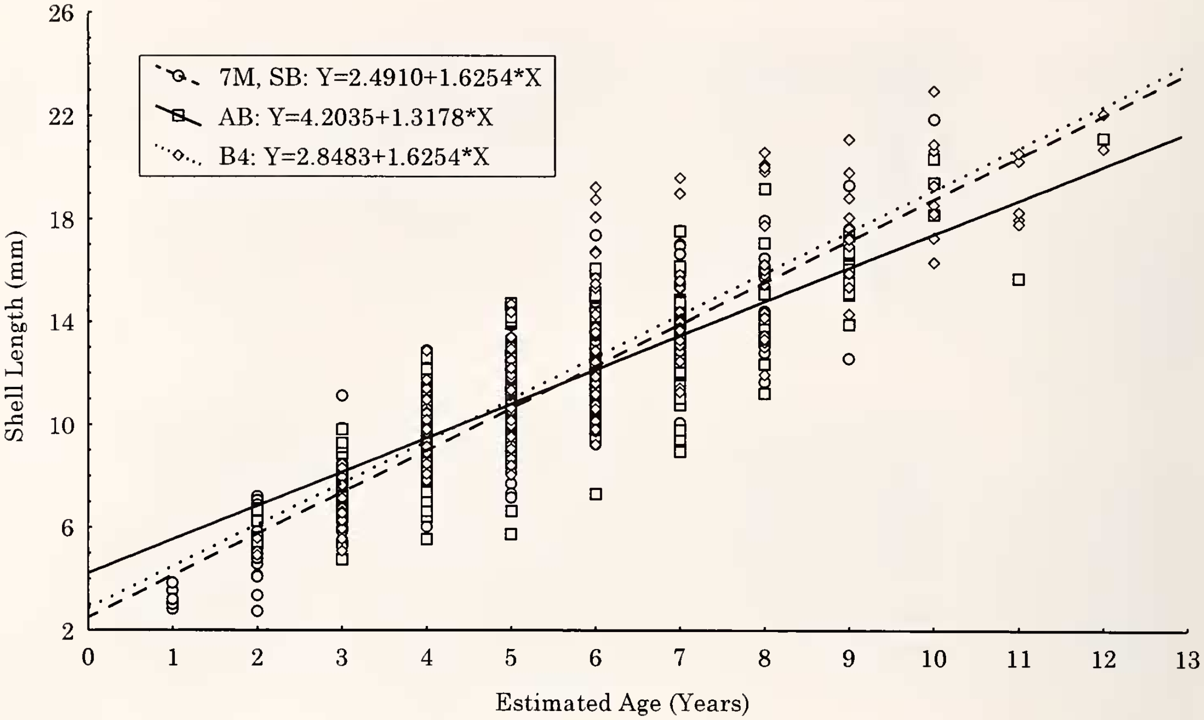

Figure 5

Regression lines for estimated age and shell length of *Tectura persona* for the four sites in Port Valdez, Alaska.

lation analysis between monthly average abundance of limpets (ind. m^{-2} for each site) and environmental variables revealed significant positive correlations ($p < 0.0031$) of *T. fenestrata* abundance to air and water temperatures and a negative correlation to salinity; other species did not show significant correlations to the environmental variables (Table 4).

Tectura persona demonstrates a seasonally distinct reproductive cycle. Developing gametes occurred throughout most of the year from spring to fall (Figure 4). Ripe gametes were observed at all sites in late August or September, and spawning generally began in October. Limpets spawned at similar times throughout the fjord. Some spawning was observed in spring and summer by limpets larger than 11 mm.

Regression analyses of growth data indicate significant relationships between age and length for *T. persona.* Shell lengths varied from 2.7 mm to 22.9 mm with a mean of 11.2 mm, and estimated age ranged from 1 to 12 years with a mean of 5.3 years. Three separate regression lines were necessary to describe the age to length relationship for the four sites (Table 5, Figure 5). The regression equations fit to 7M and SB length data were coincident. The intercept of the equation for the B4 was significantly higher ($p < 0.05$) than the equation for 7M and SB, indicating a slightly larger limpet population. The higher intercept and lower slope of the regression model for the AB site suggests larger juvenile limpets may be recruiting into the interidal population but that they are growing more slowly (in length) than at the other three sites. Regression analyses demonstrated that the relationships of both length and age to tidal height were not significant.

DISCUSSION

Inferences based on limpet abundance data agree with conclusions reached by other investigators. Field observations suggest that *T. persona* is reclusive and demonstrates negative phototactic behavior, as also noted for this species by Lindberg et al. (1975). Also, the distribution of the six intertidal limpets within Port Valdez shows similarities to those reported for these species elsewhere along the Pacific coast (Fritchman, 1961:b, c, 1962; Lindberg, 1981, 1982). While all limpets are exposed to low salinities (approaching 0‰) in summer, and low temperatures in winter, only *T. fenestrata* demonstrates a relationship between abundance values and environmental parameters. Changes in abundance of *T. fenestrata* with temperature suggests increased cryptic behavior and/or migration down the shore to avoid exposure to subfreezing air temperatures during low tides in winter.

Tectura fenestrata and *T. persona* in San Francisco Bay, California, USA, are reproductively active (includes developing stages as well as spawning activity) during winter but are quiescent in summer when water temperatures are high (Fritchman, 1961b, 1962). In Port Valdez, near the northern extreme of the range of *T. persona,* this limpet is reproductively active year-round with gonad development in spring and summer and spawning primarily from November through January (including the period of coldest temperatures; Figure 2). Large limpets (> 11 mm) spawn in summer as well, which indicates that they retain sufficient energy stores following winter to fuel gamete maturation and spawning in summer. It is presumed that smaller limpets do not retain the necessary energy stores for spawning in summer, and feeding in summer is required to provide sufficient energy for the final stages of gametogenesis prior to spawning in winter. Assessment of fresh tissues from *T. fenestrata* also indicated year-round reproductive activity with fall and winter spawning (Feder et al., 1992). The summer water temperatures in Port Valdez are considerably lower than the summer water temperatures of California, and infrequently approach the critical water temperature (approximately 13°C) considered to limit reproduction of *T. fenestrata* and *T. persona* by Fritchman (1962). This year-round reproductive period for these two limpets in Port Valdez lends support to the conclusions of Fritchman that high water temperatures (> 13°C) limit their reproductive activity (See also Underwood, 1979; Branch, 1981). In the southern range of these limpets, reduction of food resources in hot summer months (e.g., desiccation of unicellular algae growing as a film on bare surfaces; Cubit, 1984) may be important in limiting reproduction but such conditions are rare in Port Valdez. In contrast, reproductive processes are strongest in winter, in spite of the lack of food resources, suggesting that food limitations have minimal influences on the reproductive cycle of *T. persona* and *T. fenestrata.*

Similar to *T. persona* and *T. fenestrata,* year-round reproductive activity (including gametogenic development and spawning) is also described for the mussel *Mytilus trossulus* (Gould, 1850) in Port Valdez (Blanchard & Feder, 1997). Clarke (1987) noted that in polar regions, growth and reproduction are limited by the food supply, and gonad production may require two summer periods for completion. Likewise, it is possible that in addition to the lack of temperature constraints, the extended developmental periods observed in *T. persona, T. fenestrata,* and *M. trossulus* may reflect responses to the climatic patterns in Port Valdez that are similar to but less extreme than adaptations described for polar organisms.

Regression of shell growth against estimated age indicates a slow-growing *T. persona* population with moderate longevity. While the shell length to estimated age relationship of this species from Port Valdez appears to exhibit a slight curvature reflective of a nonlinear growth pattern, no concave models adequately fit the data. Thus it is concluded that the growth relationship of adult *T. persona* in Port Valdez is nearly linear over the range of lengths recorded. The moderate slopes (e.g., growth rate coefficients; Table 5) of the estimated regression functions of 1.3 to 1.6 and an observed maximum age of 12 years agrees in principle with Branch (1981) who indicated that limpets (including *T.* [*Notoacmea*] *persona* and other lottid limpets) with low growth coefficients live longer. Studies of limpet shell growth indicate it is not uncommon for differences in shell growth rate and shell size to occur, due to responses by limpets to natural environmental conditions (Branch, 1981). The differences in shell growth rate and shell sizes observed between sites in this study are well within the range of differences expected as a response to natural conditions (e.g., Branch, 1981; Hobday, 1995). Determination of annual growth rings appears to be a valid aging tool for limpets in Prince William Sound, although marking studies were not conclusive in demonstrating errors in estimated ages. However, Kenny (1968) concluded that the dominant shell ridges of *T. persona* from Oregon, USA, were annual growth rings. Additionally, shell growth ring analysis was successfully used for aging the barnacle *Semibalanus balanoides* (Linnaeus, 1767) in Port Valdez (Rucker, 1983), a number of bivalve species in Prince William Sound, including the mussel *M. trossulus* (Feder & Keiser, 1980; Blanchard & Feder, 2000), the littleneck clam *Protothaca staminea* (Conrad, 1857) (Paul & Feder, 1973), and the soft-shell clam *Mya arenaria* Linnaeus, 1758 (Feder & Paul, 1974), as well as eight other bivalve species in the southeastern Bering Sea (McDonald et al., 1981). In all of the latter Alaskan species, growth checks on shells reflected cessation of growth from reduced food resources associated with harsh winter conditions.

There is no obvious relationship between shell length or estimated age and tidal height for *T. persona* in Port Valdez. In a study of another limpet of the family Lottidae, *L. digitalis,* Hobday (1995) found few small limpets in a sheltered area along the California coast, compared to a more exposed area nearby. That study suggested that migration of larger limpets across the exposure gradient was the main source of recruitment to the sheltered region. There may have been decreased survival for juvenile and small limpets in the sheltered area as a result of reduced wave splash. In Port Valdez, small and large adult *T. persona* were distributed throughout the mid to high tidal ranges and there was no evidence of reduced survival of smaller adults in the higher tidal regions. Compared to the study site in California (Hobday, 1995), the distribution of limpets in Port Valdez may be a result of reduced risk of desiccation for the smaller individuals due to local environmental conditions (e.g., shading of sites, cloudy weather, and a wet climate) although interspecific habitat tolerances may explain some of the differences between the two studies. However, juveniles appear in spring and early summer in Port Valdez and there did appear to be a movement of juveniles (< 5 mm) up-shore with increased size as juveniles were much less common at higher tidal levels.

One objective of the present study was to compare the distribution of limpets at a site within the marine terminal area (Station B4) with the distribution of limpets at sites outside the terminal area. After the oil spill by the *Exxon Valdez* in 1989, Highsmith et al. (1996) and Hooten & Highsmith (1996) observed decreased numbers of limpets on contaminated beaches. Additionally, Liu & Morton (1998) determined that limpets (*Patelloida* species) in highly polluted waters (primarily untreated sewage) allocate more energy to reproduction, occur in lower densities, and have larger shell sizes than limpets in unaffected regions. In the present study, even when the B4 site was sampled 1 month following a minor crude oil spill in the terminal area (January 3, 1989, Alyeska Pipeline Service Company, personal communication), limpet abundance values at B4 were similar to those of the other sites. In general, the abundance and reproductive patterns of limpets at B4 were no different from these parameters at the 7M, AB, and SB sites. The slightly increased shell lengths of *T. persona* at B4 are well within the range of differences expected as a response to natural environmental conditions. Other intertidal investigations in the vicinity of B4 demonstrated a relatively robust community at B4 (Feder & Bryson-Schwafel, 1988; Jewett et al., 1993).

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